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An interfacial approach to regional segregation of two competing species mediated by a predator

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Abstract. We consider the coexistence problem of two competing species mediated by the presence of predator. We employ a reaction-diffusion model equation with Lotka-Volterra interaction, and speculate that the possibility of coexistence is enhanced by exploiting the differences in the diffusion rates of the prey and its predator. In the limit where the diffusion rates of the prey tend to zero, a new equation is derived and the dynamics of spatial segregation is discussed by using the interfacial dynamics approach. Also, we show that spatial segregation exhibits periodic and chaotic dynamics for certain parameter ranges.

1. Introduction

In some circumstances, predation may have a tendency to increase species diversity in competitive communities, which is called predation-mediated coexistence. This phenomenon can be intuitively understood as follows: Under the situation where there are two competing species and one would normally become extinct due to competition from the other, coexistence of these species is possible if a predator is present and exerts higher predation pressure on a competitively dominant species. In fact, such coexistence is shown in experiments and observations (Connell [3], Paine [19], for instance).

Along this line, numerous theoretical studies have been done by using Lotka-Volterra models. The simplest model is the following ODEs of two-competing species and one predator:

$$(1.1) \quad \begin{cases} \frac{du_1}{dt} = f_1(u_1, u_2, v)u_1 \\ \frac{du_2}{dt} = f_2(u_1, u_2, v)u_2 \\ \frac{dv}{dt} = g(u_1, u_2, v)v \end{cases}$$

with

$$\begin{cases} f_1(u_1, u_2, v) = a_1 - b_1 u_1 - c_1 u_2 - k_1 v \\ f_2(u_1, u_2, v) = a_2 - c_2 u_1 - b_2 u_2 - k_2 v \\ g(u_1, u_2, v) = -r + \alpha_1 k_1 u_1 + \alpha_2 k_2 u_2, \end{cases}$$

where $u_1(t)$, $u_2(t)$ and $v(t)$ are respectively the spatial averaged densities of two competing species and its predator at time $t > 0$. Here, a_i , b_i and c_i are respectively the intrinsic growth rate, the intra- and inter-specific competition rates of u_i , k_i is the predation rate of v , α_i is the transformation rate of predation ($i=1,2$), and r is the death rate of v . All of them are positive constants. Fix the parameters a_i , b_i and c_i ($i=1,2$) so that one of the species becomes always extinct in the absence of the predator ($v \equiv 0$). Then, it is known that predation-mediated coexistence is possible depending on the choice of values of the rest parameters. The asymptotic states of coexistence can be classified into three types: (i) equilibrium states, (ii) periodic solutions and (iii) chaotic behavior. The last two patterns show temporal segregation between two competing species (Fujii [5], Takeuchi and Adachi [20], Mimura and Kan-on [13], for instance).

On the other hand, recently the migrating effect of species on such coexistence has also been investigated. Suppose that all migration occurs solely by usual diffusion. The resulting model is represented by the following reaction-diffusion system:

$$(1.2) \quad \begin{cases} \frac{\partial u_1}{\partial t} = d_1 \Delta u_1 + f_1(u_1, u_2, v) u_1 \\ \frac{\partial u_2}{\partial t} = d_2 \Delta u_2 + f_2(u_1, u_2, v) u_2 \\ \frac{\partial v}{\partial t} = D \Delta v + g(u_1, u_2, v) v, \end{cases} \quad t > 0, \quad x \in \Omega$$

where d_i and D are respectively the diffusion rates of u_i and v ($i=1,2$), and Δ is the Laplace operator in \mathbf{R}^n . The habitat Ω is a bounded domain with smooth boundary $\partial\Omega$. The boundary condition is assumed to be the zero flux one:

$$(1.3) \quad \frac{\partial u_i}{\partial n} = 0 \quad (i=1,2), \quad \frac{\partial v}{\partial n} = 0, \quad t > 0, \quad x \in \partial\Omega,$$

where $\frac{\partial}{\partial n}$ is the outward normal derivative on $\partial\Omega$. For the problem (1.2) with (1.3), if the diffusion rates d_1 , d_2 and D are all large, then u_1 , u_2 and v become spatially homogeneous for large time, that is, the dynamics of solutions can be completely analyzed by solving (1.1). Suppose that two competing species can never coexist even in the presence of predator, if all of the diffusion rates are large. We now address the following question: Is there any possibility of coexistence for two competing species if all of the diffusion rates are not necessarily large? Under this situation, Mimura and Kan-on [13] and Mimura et al. [14] have shown that predation-mediated coexistence is possible by exploiting the differences in the diffusion rates of the prey and its predator. This implies that the possibility of coexistence for two competing species exhibiting spatially segregating patterns is enhanced by the interaction of predation pressure and diffusion effect. The asymptotic states are classified into three cases: (i) stationary patterns exhibiting spatial segregation (Figure 1.1), (ii) time-periodic patterns exhibiting spatio-temporal segregation (Figure 1.2) and (iii) non periodic-oscillating patterns exhibiting spatio-temporal segregation (Figure 1.3).

Especially when both d_1 and d_2 are sufficiently small compared with D , singular perturbation analysis is applied to show that there is striking spatial segregation in the two competing species. As shown in Figures 1.1 ~ 1.3, we can see that time-dependent internal layers appear which separate two different regions where one of the species is dominant due to strong competition. From segregating pattern view point, we are interested in studying the dynamics of such internal layer. To do it, a new system, which is called the segregating interface equation of competing species, can be derived from the RD system (1.2) in the limits when d_1 and d_2 tend to zero.

The purpose of this paper is to study spatial segregation of competing species by using the above interface equation.

2. Models and assumptions

We use the following non-dimensional variables and parameters:

$$\begin{aligned}\bar{t} &= \frac{t}{\delta} \quad (\delta = \frac{c_1}{a_1 \alpha_2 k_2}), \quad \bar{u}_1 = \frac{c_2}{a_2} u_1, \quad \bar{u}_2 = \frac{c_1}{a_1} u_2, \quad \bar{v} = \frac{k_2}{a_2} v, \\ \alpha &= \frac{a_2 b_1}{a_1 c_2}, \quad \beta = \frac{a_1 b_2}{a_2 c_1}, \quad \kappa = \frac{a_2 k_1}{a_1 k_2}, \quad \gamma = \frac{\alpha_1 c_1}{\alpha_2 c_2}, \\ \bar{\alpha}_1 &= \delta a_1, \quad \bar{\alpha}_2 = \delta a_2, \quad \bar{r} = \delta r, \quad \varepsilon = \delta d_1, \quad d = \frac{d_2}{d_1}, \quad \bar{D} = \delta D.\end{aligned}$$

Then, (1.2) becomes

$$(2.1) \quad \begin{cases} \frac{\partial u_1}{\partial t} = \varepsilon \Delta u_1 + a_1 f_1(u_1, u_2, v) u_1 \\ \frac{\partial u_2}{\partial t} = \varepsilon d \Delta u_2 + a_2 f_2(u_1, u_2, v) u_2 \\ \frac{\partial v}{\partial t} = D \Delta v + g(u_1, u_2, v) v \end{cases}$$

with

$$\begin{cases} f_1(u_1, u_2, v) = 1 - \alpha u_1 - u_2 - \kappa v \\ f_2(u_1, u_2, v) = 1 - u_1 - \beta u_2 - v \\ g(u_1, u_2, v) = -r + \kappa \gamma u_1 + u_2, \end{cases}$$

where we drop the overbars of all variables and parameters.

Assume that

$$(A-1) \quad k > 1,$$

which indicates that the predator prefers to eat u_1 -species rather than u_2 -species.

We first consider a simple case of (2.1) when v is fixed to be a constant satisfying $0 < v < \frac{1}{k}$:

$$(2.2) \quad \begin{cases} \frac{\partial u_1}{\partial t} = \varepsilon \Delta u_1 + a_1((1-kv) - \alpha u_1 - u_2)u_1 \\ \frac{\partial u_2}{\partial t} = \varepsilon d \Delta u_2 + a_2((1-v) - u_1 - \beta u_2)u_2. \end{cases}$$

Under the zero flux boundary conditions, it has been already shown in de Mottoni [4] and Hsu [7] that

(a) if $\frac{1}{\beta}, \alpha < \frac{1-kv}{1-v}$, then $E_{+o}(v) = \left(\frac{1-kv}{\alpha}, 0\right)$ is globally stable,

(b) if $\frac{1-kv}{1-v} < \frac{1}{\beta}, \alpha$, then $E_{o+}(v) = \left(0, \frac{1-v}{\beta}\right)$ is globally stable,

(c) if $\frac{1}{\beta} < \frac{1-kv}{1-v} < \alpha$, then $E_{++}(v) = \left(\frac{(1-kv)\beta - (1-v)}{\alpha\beta - 1}, \frac{\alpha(1-v) - (1-kv)}{\alpha\beta - 1}\right)$ is globally stable,

(d) if $\alpha < \frac{1-kv}{1-v} < \frac{1}{\beta}$, then $E_{+o}(v)$ and $E_{o+}(v)$ are both locally stable.

The case (d) is more precisely investigated. When Ω is convex, any non-constant equilibrium solutions are unstable even if they exist, that is, $E_{+o}(v)$ and $E_{o+}(v)$ are only stable equilibria of (2.2) (Kishimoto and Weinberger [10]). On the other hand, when Ω is suitably non-convex, there are stable non-constant equilibrium solutions in addition to the aboves (Matano and Mimura [12]). This indicates that coexistence of two competing species is possible due to the domain-shape of Ω .

In this paper, we take Ω to be convex for simplicity, and we assume that

$$(A-2) \quad \alpha < 1 < \beta,$$

$$(A-3) \quad \alpha\beta < 1.$$

Under the assumptions (A-1) ~ (A-3), the lines of $(1-kv)-\alpha u_1-u_2=0$ and $(1-v)-u_1-\beta u_2=0$ are classified into the above three cases (a), (b) and (d) depending on the value of v as in Figure 2.1. The coexistence equilibrium (Case (c)) does not occur for any v . For small v , u_2 -species becomes always extinct due to competition (Case (a)). For large v but less than $\frac{1}{k}$, the predation pressure on u_1 -species is so strong that u_1 -species becomes always extinct due to competition (Case (b)). For middle v , $E_{+0}(v)$ and $E_{0+}(v)$ are locally stable (Case (d)).

Come back to the original system (2.1). If ε and D are both very large, then (u_1, u_2, v) becomes spatially homogeneous and the asymptotic behavior of solutions is determined by that of the following ODEs:

$$(2.3) \quad \begin{cases} \frac{\partial u_1}{\partial t} = a_1(1-\alpha u_1-u_2-kv)u_1 \\ \frac{\partial u_2}{\partial t} = a_2(1-u_1-\beta u_2-v)u_2 \\ \frac{\partial v}{\partial t} = (-r+k\gamma u_1+u_2)v. \end{cases}$$

Fix k , α and β to satisfy (A-1) ~ (A-3). We denote by E_{000} , E_{+00} and E_{0+0} the equilibrium points $(0,0,0)$, $(\frac{1}{\alpha}, 0, 0)$ and $(0, \frac{1}{\beta}, 0)$ of (2.3), respectively.

Other equilibrium points are also suitably denoted by E_{+0+} , E_{0++} and E_{+++} . When γ and r are adjustable parameters, the existence region of the positive equilibrium E_{+++} in (γ, r) -space is given by the shaded triangular regions in Figure 2.2, where $r^* = \frac{k-1}{\beta k-1}$ and $\gamma^* = \frac{k-\alpha}{k(k\beta-1)}$ ([13] and [14]).

The region when $\gamma > \gamma^*$ corresponds to $|A| < 0$ while the region when $\gamma < \gamma^*$ does to $|A| > 0$, where $A = \begin{pmatrix} \alpha & 1 & k \\ 1 & \beta & 1 \\ -k\gamma & 1 & 0 \end{pmatrix}$. For any fixed γ , the global

pictures of equilibria of (2.3) with respect to r are drawn in Figure 2.3 .

We are concerned with the case $|A| < 0$, where E_{+++} is unstable (Figure 2.3 (b)). In the ecological terms, this case is interpreted as follows, depending on the death rate of the predator:

(i) there are no stable positive equilibria for any r ;

- (ii) when r is small ($r < r_0 = r_0(\gamma) = \frac{k(k-1)}{k-\alpha}\gamma$), the predation pressure of v on u_1 is so strong that u_1 -species becomes extinct and only (u_2, v) -species coexists;
- (iii) when r is middle ($r_0 < r < r^*$), where either (u_1, v) -species or (u_2, v) -species coexists;
- (iv) when r is large ($r^* < r < \bar{r} = \bar{r}(\gamma) = \frac{k\gamma}{\alpha}$), the predation pressure of v on u_1 is so weak that u_2 -species becomes extinct while u_1 -species and the predator v exist;
- (v) when r becomes larger ($\bar{r} < r$), the predator v becomes extinct and only u_1 -species exists.

Consequently, under the assumptions (A-1) ~ (A-3), if the diffusion rates of all species are very large, they become spatially homogeneous so that predation-mediated coexistence never occurs except for the shaded region above γ^* . Now, the following problem arises: whether coexistence of three species is possible or not by taking spatial pattern if some of the diffusion rates are not large? Mimura et al. [13], [14] suggest that coexistence of two competing species is possible when the diffusion rates of the two species ε and εd are small compared with that of the predator D . Especially, when ε is sufficiently small, there appear internal layers with width of the order $O(\sqrt{\varepsilon})$ in the solutions u_1 and u_2 , by which spatial segregation is clearly observed as shown in Figures 1.1 ~ 1.3.

In the next section, to understand the dynamics of such layers, we take the limit $\varepsilon \downarrow 0$ in the system (2.1), by which these layers can be regarded as interfaces, and derive a segregating interface equation for competing species from (2.1).

3. Interface equation

For simplicity only, we assume that the habitat Ω is a 2-dimensional bounded domain. Assume first that v is a constant to satisfy

$$(3.1) \quad \frac{\beta-1}{k\beta-1} < v < \frac{1-\alpha}{k-\alpha}.$$

We consider the system (2.2) for (u_1, u_2) . Then, the dynamics in (2.2) implies Case (d), that is, $E_{+0}(v)$ and $E_{0+}(v)$ are both locally stable. In addition to the above, we assume that the competitive dynamics is so strong compared with the migration of the species in the sense that $a_i = \frac{\theta_i}{\varepsilon}$ ($i=1,2$) with some constants θ_i and sufficiently small ε . Under this situation, one could intuitively understand that the evolution process of the dynamics consists of two stages. The first one is the occurrence of competitive exclusion in a short time period. We observe that for smooth initial distributions $(u_1(0, x), u_2(0, x)) = (\phi_1(x), \phi_2(x))$, the diffusion terms $\varepsilon \Delta u_1$ and $\varepsilon \Delta u_2$ may be negligible, so that (2.2) is approximated by

$$(3.2) \quad \begin{cases} \frac{\partial u_1}{\partial t} = \frac{\theta_1}{\varepsilon} ((1-kv) - \alpha u_1 - u_2) u_1 \\ \frac{\partial u_2}{\partial t} = \frac{\theta_2}{\varepsilon} ((1-v) - u_1 - \beta u_2) u_2. \end{cases}$$

Therefore the habitat Ω is decomposed into two disjoint regions, namely a u_1 -dominant region $\Omega_1(t)$ where $(u_1, u_2) \approx E_{+0}(v)$ and a u_2 -dominant region $\Omega_2(t)$ where $(u_1, u_2) \approx E_{0+}(v)$. This indicates the occurrence of segregating interface $\Gamma(t)$ between two competing species. How is the dynamics of $\Gamma(t)$? This is the second stage. We note that $\varepsilon \Delta u_1$ and $\varepsilon \Delta u_2$ can no longer be neglected in a neighborhood of interfaces, so that (3.2) is not valid there. To study it, the limiting equation as $\varepsilon \downarrow 0$ can be derived. (For the derivation, we refer to the papers by Kuramoto [11] and Ohta [17].) It is described by

$$(3.3) \quad \frac{\partial \Gamma}{\partial t} = (c(v) - \varepsilon v(v) \kappa) \mathbf{n},$$

where κ is the mean curvature of $\Gamma(t)$ and \mathbf{n} is the normal vector of $\Gamma(t)$ pointing from $\Omega_1(t)$ to $\Omega_2(t)$ (Figure 3.1), and $c(v)$ and $v(v)$ are defined as follows: Let $(U_1(z;v), U_2(z;v))$ ($z = x - ct$) be the 1-dimensional traveling wave solution with the velocity c which satisfies the problem

$$(3.4)_1 \quad \begin{cases} 0 = \frac{d^2 u_1}{dz^2} + c \frac{du_1}{dz} + \theta_1((1 - kv) - \alpha u_1 - u_2)u_1 \\ 0 = d \frac{d^2 u_2}{dz^2} + c \frac{du_2}{dz} + \theta_2((1 - v) - u_1 - \beta u_2)u_2, \end{cases} \quad t > 0, z \in \mathbb{R}$$

$$(3.4)_2 \quad \begin{cases} \lim_{z \downarrow -\infty} (u_1, u_2) = E_{+0} \\ \lim_{z \uparrow +\infty} (u_1, u_2) = E_{0+}. \end{cases}$$

The existence of traveling wave solutions is shown in Conley and Gardner [2], but as far as we know, the stability and uniqueness problems have not been yet completely solved. However, our numerical simulations confirm that (3.4) has a stable traveling wave solution which is unique except for spatial translation, that is, the velocity $c = c(v)$ is uniquely determined (Figure 3.2), and it is strictly monotone decreasing with v and $c(v^*) = 0$ with some v^* satisfying (3.1) (Figure 3.3). Let \mathcal{L} be the linearized operator of (3.4) around the traveling wave solution $(U_1(z;v), U_2(z;v))$ of (3.4) in the moving coordinate, that is,

$$\mathcal{L} = D_d \frac{d^2}{dz^2} + vI \frac{d}{dz} + F'(U_1, U_2),$$

where $D_d = \begin{pmatrix} 1 & 0 \\ 0 & d \end{pmatrix}$ and $F' = \left\{ \theta_i \frac{\partial(f_i \cdot u_i)}{\partial u_j} \right\}_{i,j=1,2}$. We note that \mathcal{L} has the zero

eigenvalue $\lambda_0 = 0$ since any spatial translation of $(U_1(z;v), U_2(z;v))$ is also a solution of (3.4). Let ξ_0 be the eigenfunction of \mathcal{L} associated with λ_0 . Let \mathcal{L}^* be the adjoint operator of \mathcal{L} and ξ_0^* be the eigenfunction of \mathcal{L}^* associated with λ_0 which is normalized such that $\langle \xi_0^*, \xi_0 \rangle = 1$. Now, $v(v)$ is defined by

$$v(v) = \langle \xi_0^*, D_d \xi_0 \rangle.$$

Generally, $v(v)$ depends on the value of v , however, it should be noted that $v \equiv 1$ in the special case $d=1$. We call (3.3) the segregating interface equation for two competing species for given v .

In particular, the 1-dimensional version of (3.3) is simply reduced to

$$\frac{\partial \Gamma}{\partial t} = c(v).$$

It turns out that $\Gamma(t)$ is either monotone decreasing or monotone increasing with t depending on the value of v ($\neq v^*$). However, for higher dimensional cases, the geometrical effect is taken into account in the dynamics of $\Gamma(t)$ so that the dynamics seems to be rather complex. Recently, for the case when v is constant, the study of (3.3) has been investigated by numerous authors from both theoretical and numerical view points (Grayson [6], Osher and Sethian [18], for instance).

We now come back to the original problem for (u_1, u_2, v) :

$$(3.5) \quad \begin{cases} \frac{\partial u_1}{\partial t} = \varepsilon \Delta u_1 + \frac{\theta_1}{\varepsilon} f_1(u_1, u_2, v) u_1 \\ \frac{\partial u_2}{\partial t} = \varepsilon d \Delta u_2 + \frac{\theta_2}{\varepsilon} f_2(u_1, u_2, v) u_2 \\ \frac{\partial v}{\partial t} = D \Delta v + g(u_1, u_2, v) v. \end{cases} \quad t > 0, x \in \Omega$$

Since ε is sufficiently small, the first and second equations are approximated by

$$(3.6)_1 \quad \begin{cases} 1 - \alpha u_1 - kv = 0 \\ u_2 = 0 \end{cases} \quad \text{in } \Omega_1(t)$$

and

$$(3.6)_2 \quad \begin{cases} u_1 = 0 \\ 1 - \beta u_2 - v = 0, \end{cases} \quad \text{in } \Omega_2(t)$$

respectively, where $\Omega = \Omega_1(t) \cup \Omega_2(t)$. Thus, by substituting (3.6) into the third equation for v in (3.5), it is simply represented as

$$\frac{\partial v}{\partial t} = D\Delta v + g_i(v)v \quad \text{in } \Omega_i(t) \quad (i=1,2),$$

where

$$g_i(v) = \begin{cases} \theta_1(-r + \frac{k\gamma}{\alpha}(1-kv)) & (i=1) \\ \theta_2(-r + \frac{1}{\beta}(1-v)) & (i=2). \end{cases}$$

Thus, the limiting system of (3.5) as $\varepsilon \downarrow 0$ is proposed as the following system for (Γ, v) :

$$(3.7) \quad \begin{cases} \frac{\partial \Gamma}{\partial t} = (c(v_l) - \varepsilon v(v_l)\kappa)\mathbf{n} & \text{on } \Gamma(t) \\ \frac{\partial v}{\partial t} = D\Delta v + g_i(v)v & \text{in } \Omega_i(t) \quad (i=1,2) \end{cases}$$

with the smoothness of v on interfaces

$$(3.8) \quad v(t, \cdot) \in C^1$$

(Chen [1]), where v_l is the value of v on the interface $\Gamma(t)$. With the zero flux boundary condition for v on $\partial\Omega$, we can formulate the free boundary problem (3.7) and (3.8) for (Γ, v) . If this problem can be solved, $\Gamma(t)$ gives the geometrical shape of regional segregation of two competing species and $v(t, x)$ gives the spatial profiles of u_1 and u_2 by (3.6).

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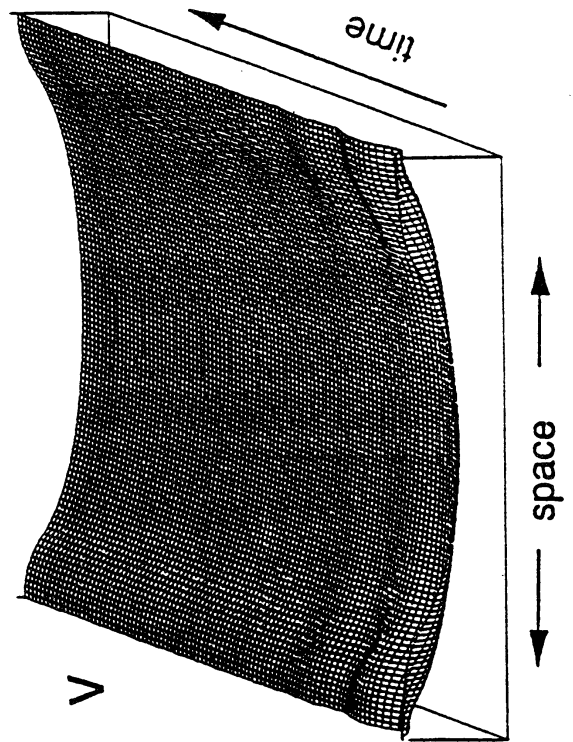
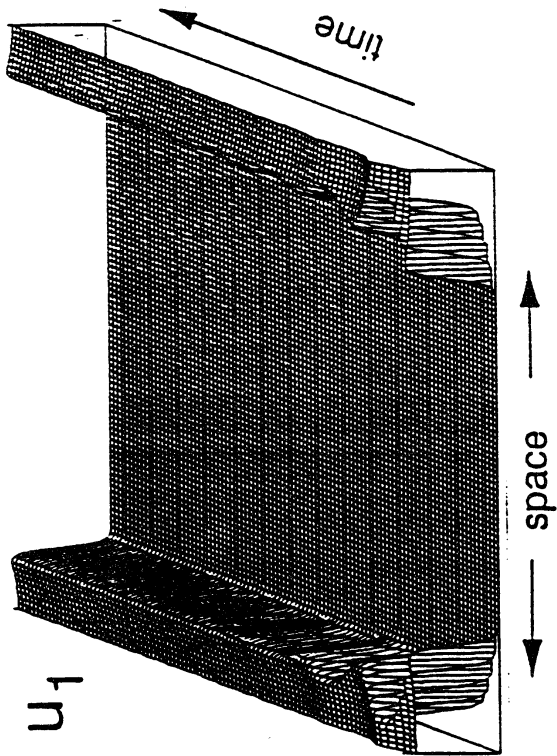
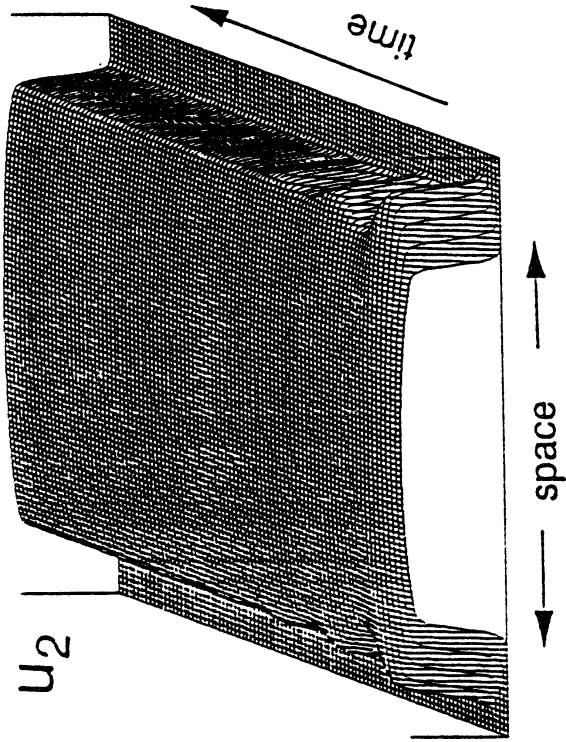


Figure 1.1. Stationary pattern

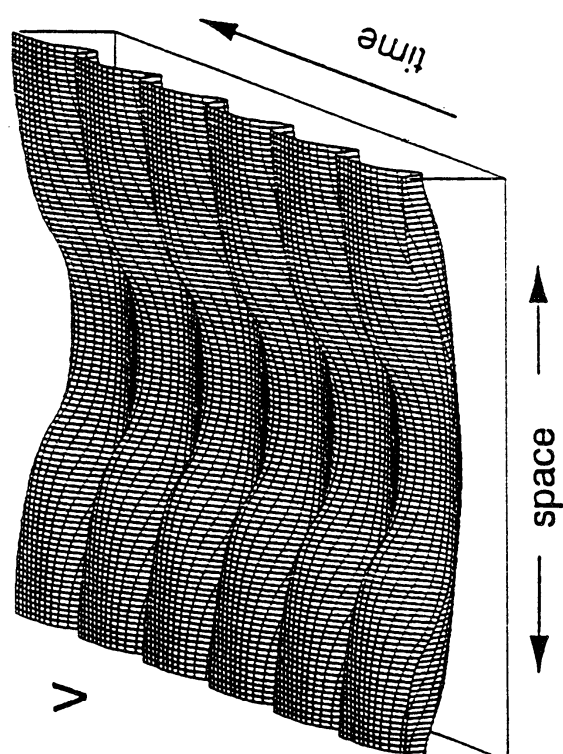
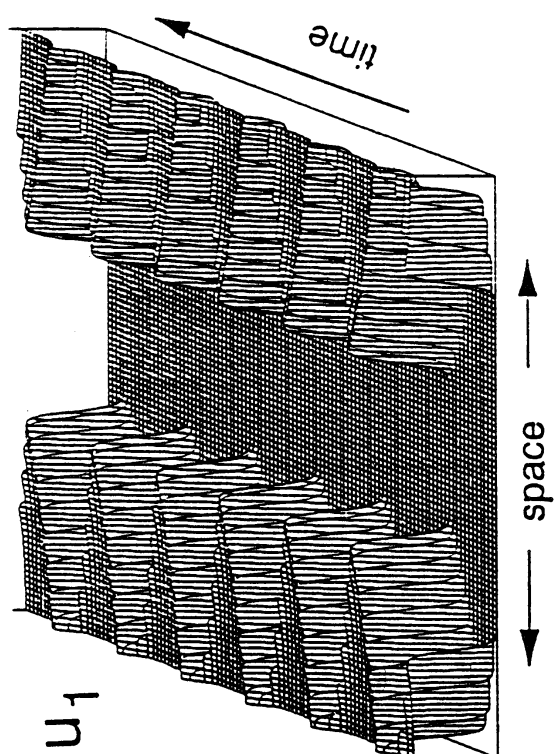
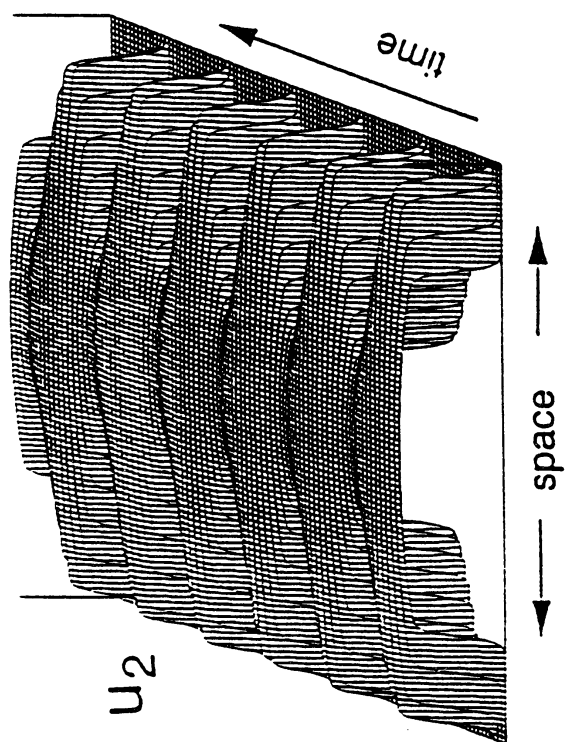


Figure 1.2. Time-periodic pattern

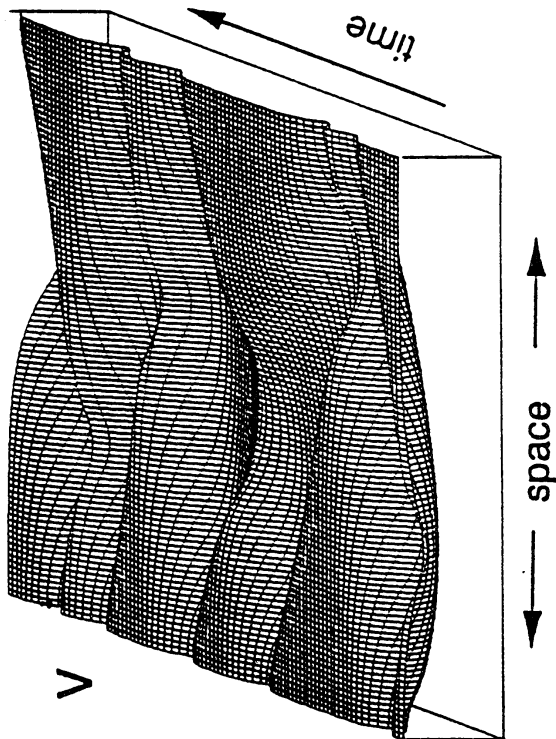
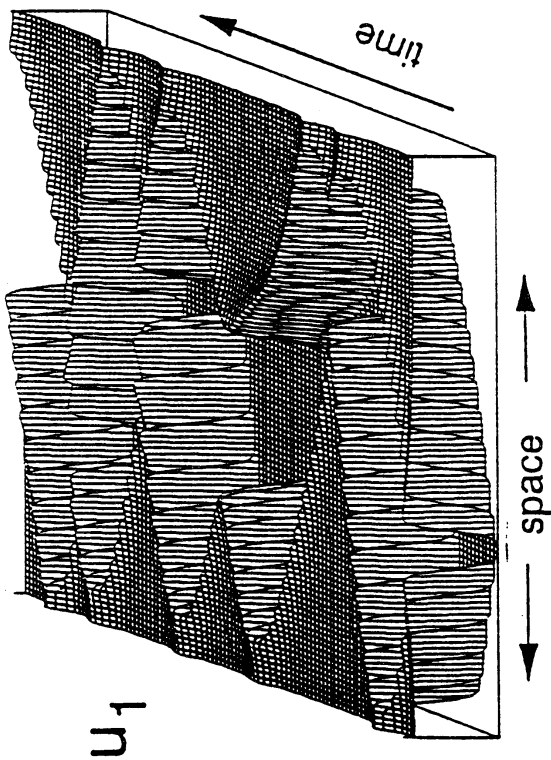
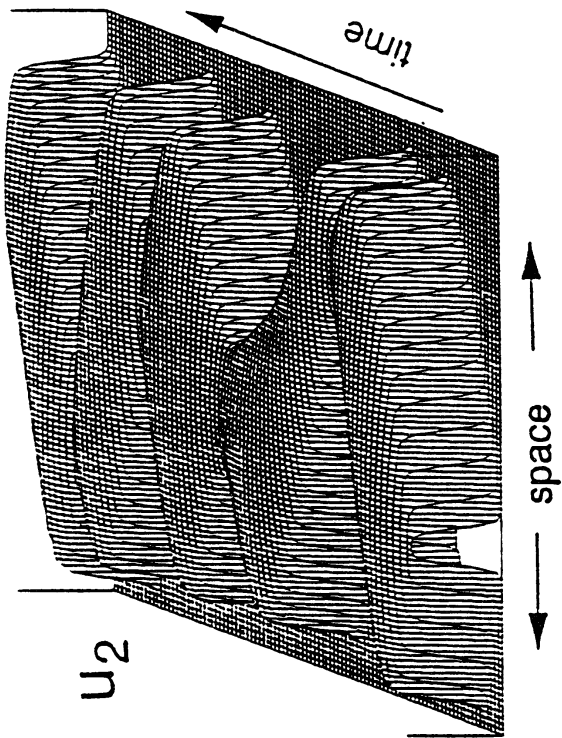


Figure 1.3. Non periodic-oscillating pattern

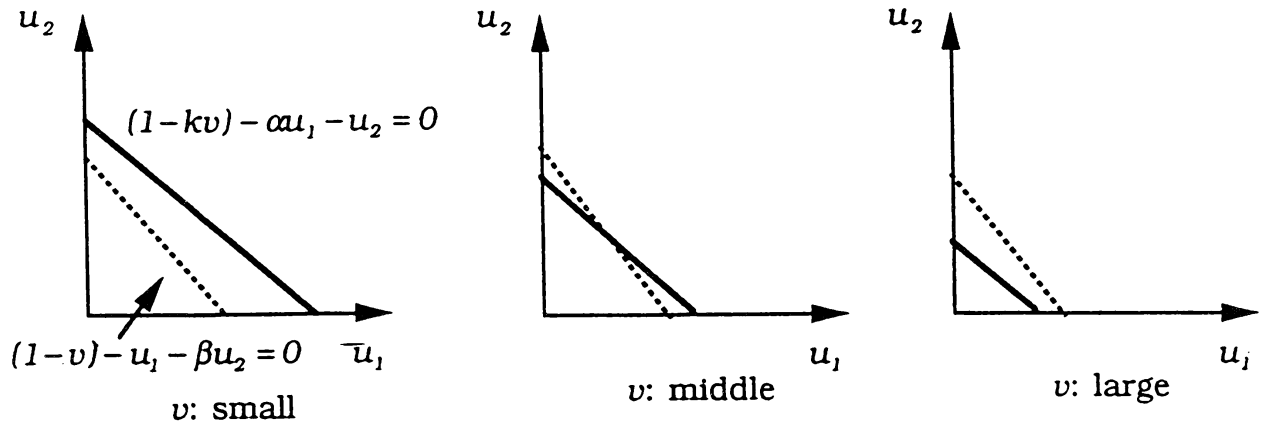


Figure 2.1. Isoclines of $(1-kv) - \alpha u_1 - u_2 = 0$
and $(1-v) - u_1 - \beta u_2 = 0$

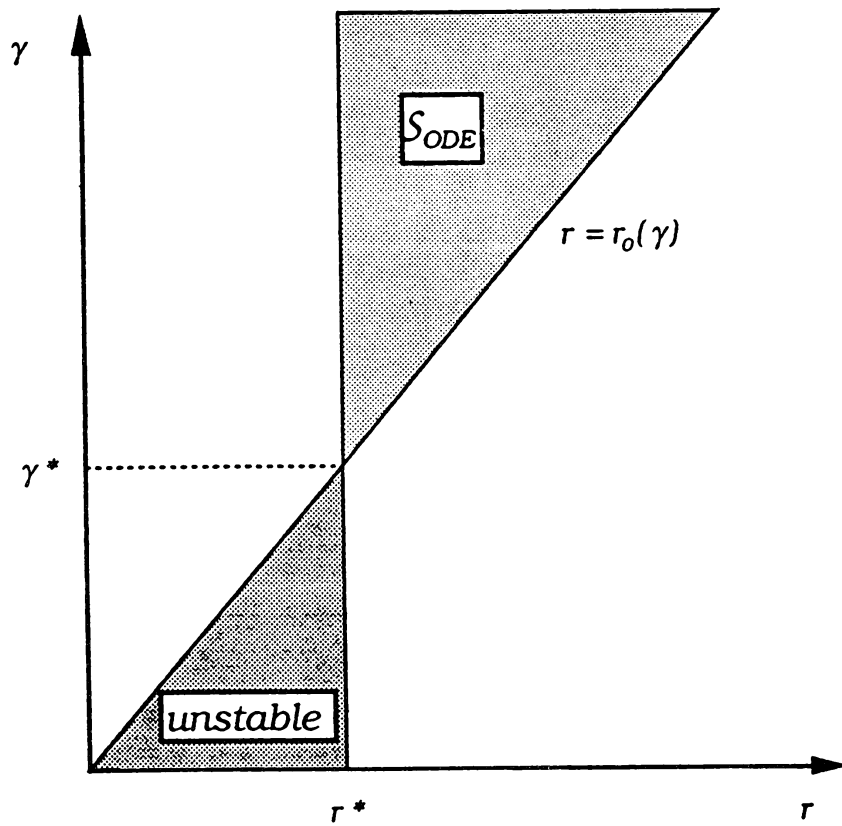


Figure 2.2. Existence region of E_{++} in (γ, r) -space

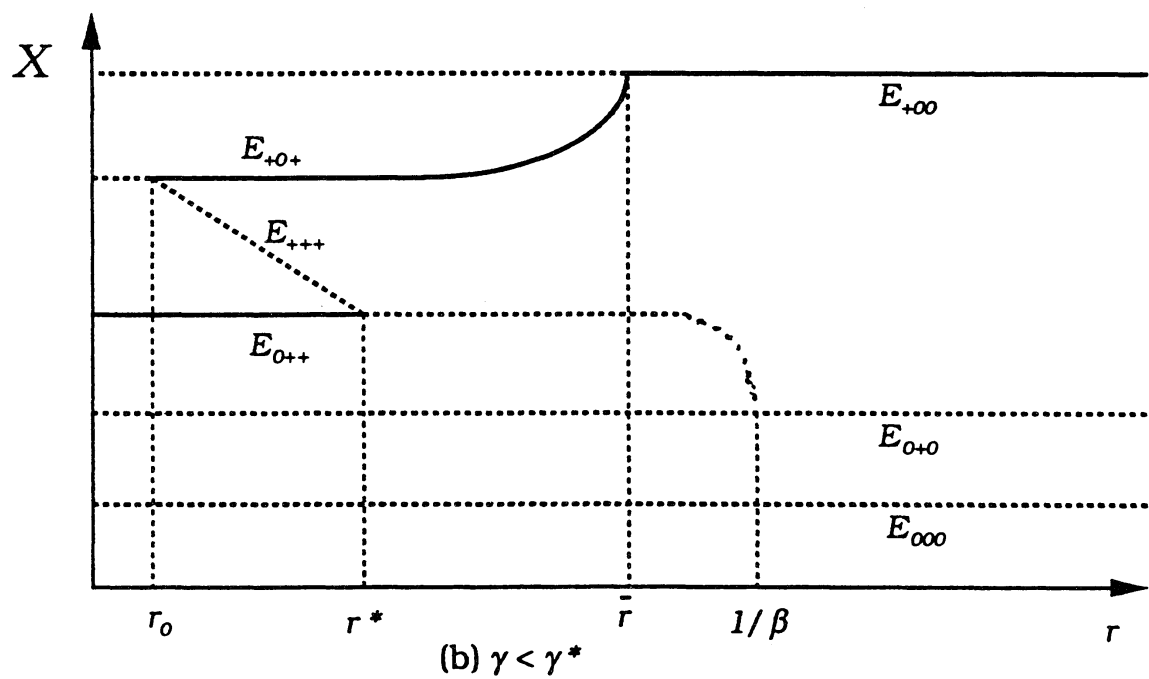
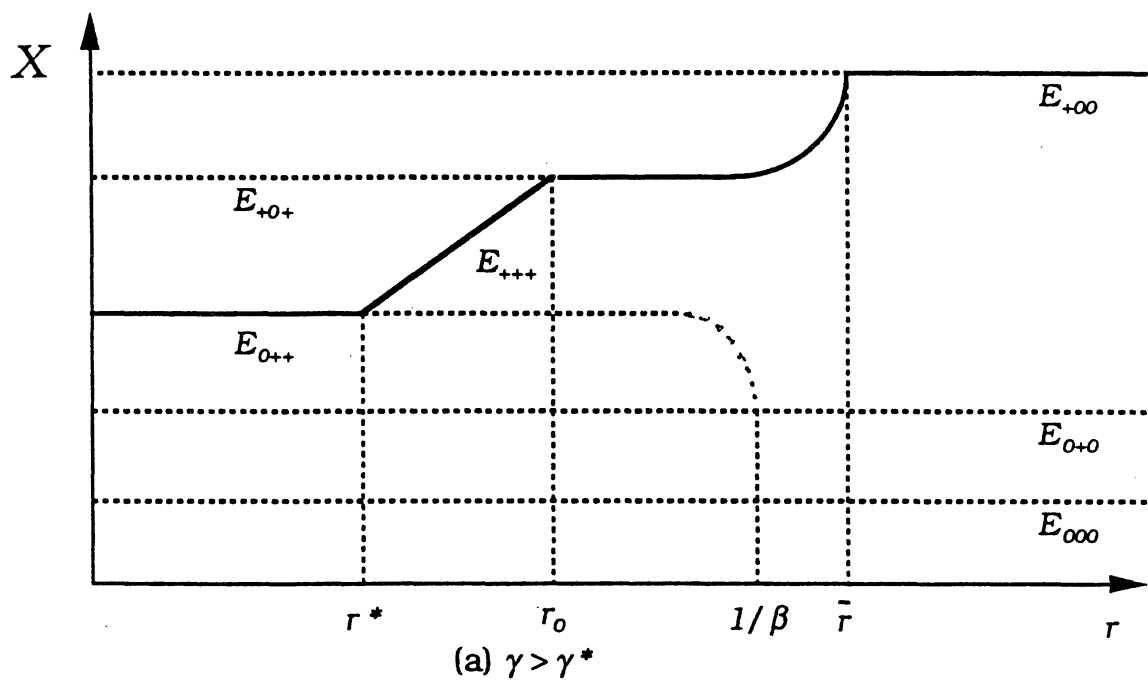


Figure 2.3. Schematic global bifurcation diagrams of equilibria with respect to r

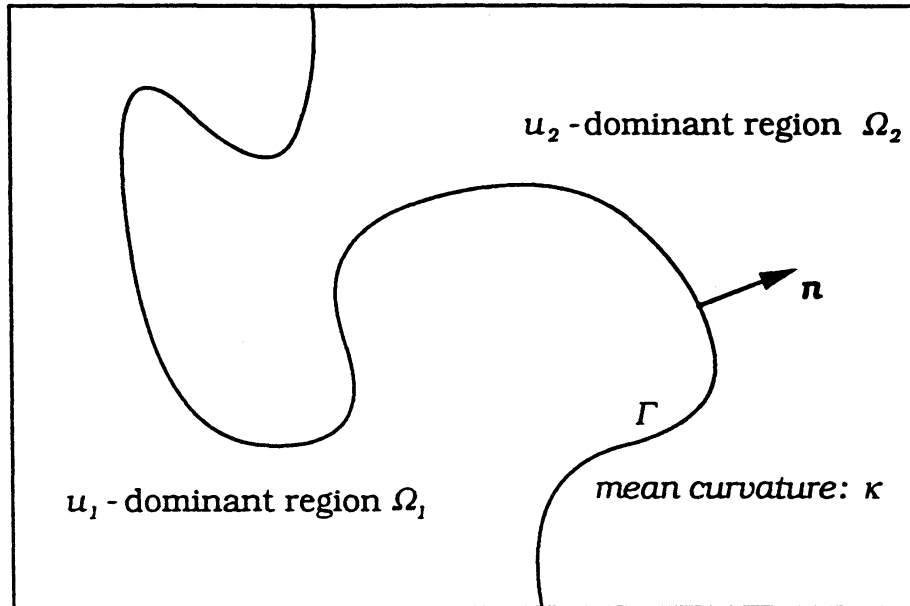


Figure 3.1. u_1 - dominant region Ω_1 , u_2 - dominant region Ω_2 and segregating interface Γ

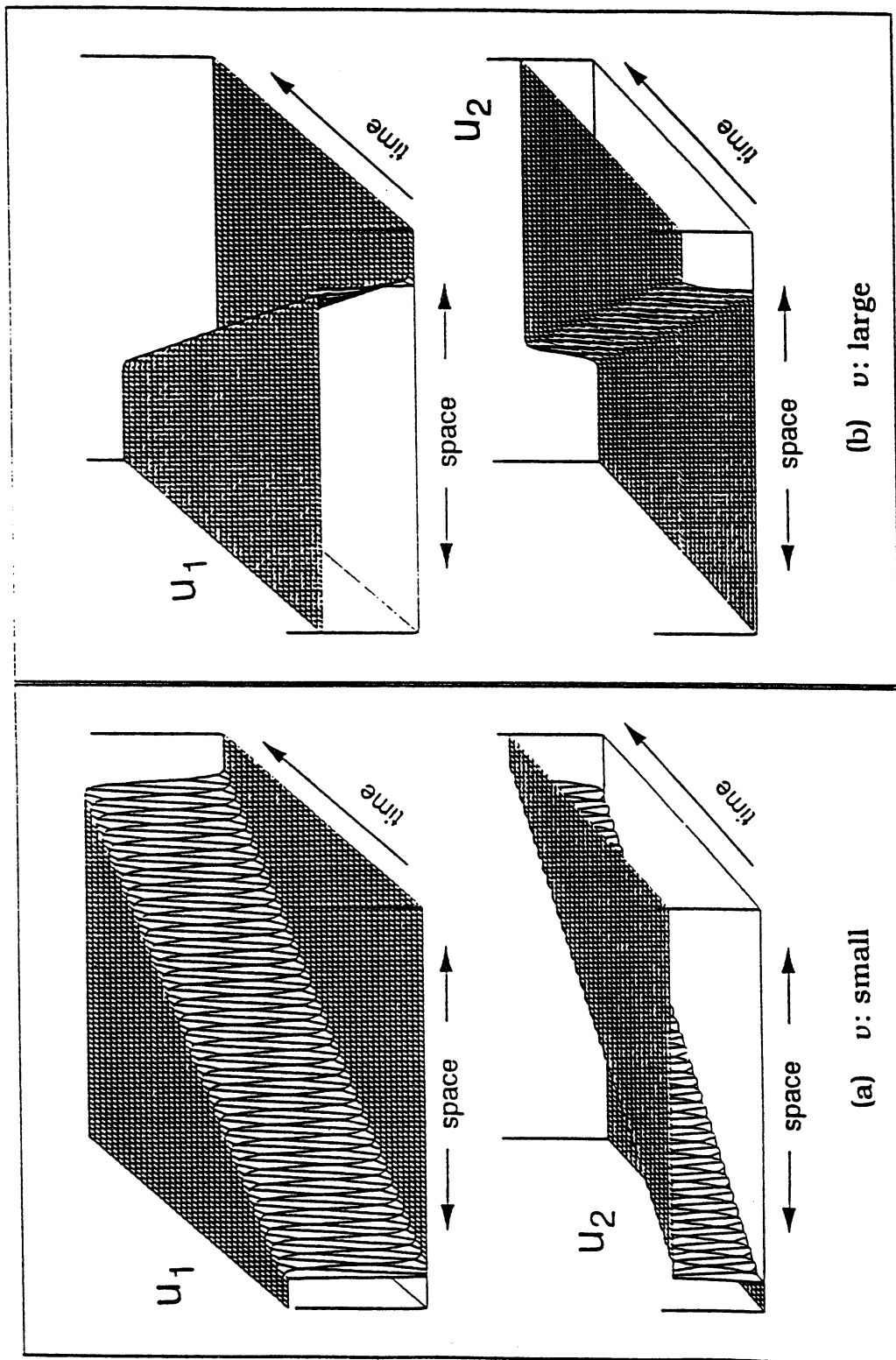


Figure 3.2. Traveling wave solutions of (3.4)

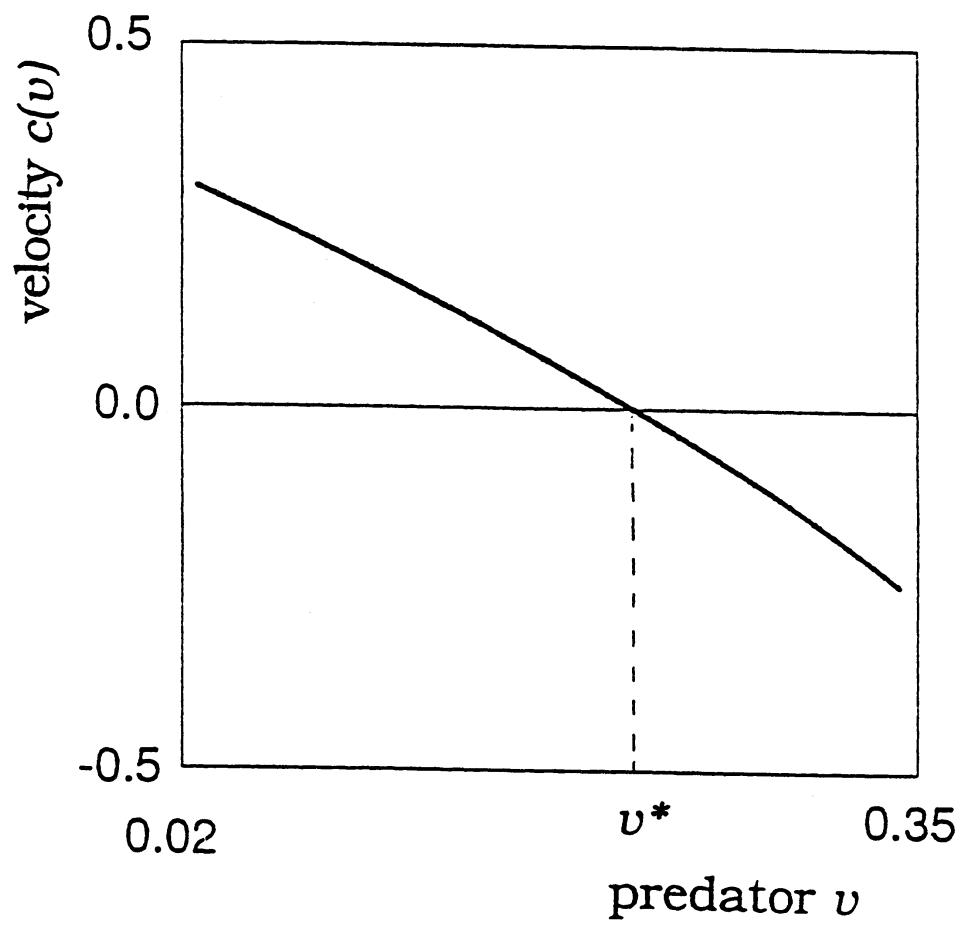


Figure 3.3. Velocity of traveling wave solutions